Why some Carnivora species ...

Background to both studies *a) Findings from previous work*

- Many captive Carnivora thrive, but some species show high levels of stereotypic behaviour (SB; mainly route-tracing, RT) & infant mortality (IM).
- When Phylogenetic Comparative Methods (PCMs) were used to compare species and identify specific intrinsic risk factors [1,2], being naturally wide-ranging emerged as a key predictor of RT [1,2].
- One study found that ranging predicted high IM too [1]; while the other suggested long chases during hunts as a second risk factor for RT [2].

I. Why does home range size predict Carnivora welfare?

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Background to the ranging behaviour study

- We aimed to identify *why* wide-ranging Carnivora species are more prone to welfare issues.
- This could help in better predicting at-risk species, and also inform future enclosure design.
- Natural annual home ranges (AHRs) are driven by many factors that we sought data on, including energy needs, predation pressure, and social organisation [3].
- Being wide-ranging has consequences too, e.g. on no. of dens used, relocations made per year, distances travelled [2,3]; and potentially on aspects of brain development, especially larger hippocampi for improved spatial learning [3]. We therefore sought data on these too.

Methods for the ranging behaviour study

- After updating the relevant databases (see poster to right; also see [2] for details), we replicated the previous work. RT was still strongly predicted by AHR (PGLS, p=0.012, $t_{1,21}$=2.45), but IM was not (PGLS, p=0.15, $t_{1,39}$=1.03). We therefore focussed on RT.
- For data on potential correlates of AHR – see Results for details - we used our extensive wild behaviour (WB) database, plus several specialised sources [4].
- First we identified which of these factors did covary with AHR in our sample.
- For those that did, the degree to which they explained the AHR effect on RT was then investigated statistically (controlling for body mass where appropriate).

Results: *What correlates of annual home range size (AHR) predict route-tracing better or more fully than AHR itself?*

Potential correlate of AHR	Does it covary with AHR?	Does it predict RT?	Does it when AHR is in the model?	Does AHR still predict?
Body mass	Yes ($p=0.00005$, $t_{1,37}$=4.27)	Yes ($p=.008$, $t_{1,22}$=1.94)	No ($p=.49$, $t_{2,38}$=0.017)	Yes ($p=0.042$, $t_{2,18}$=1.82)
Individual metabolic need	Yes ($p=1x10\text{-}6$, $t_{1,35}$=5.5)	Yes ($p=0.018$, $t_{1,20}$=2.25)	No ($p=0.32$, $t_{2,38}$=-0.49)	Yes ($p=0.032$, $t_{2,16}$=1.99)
Long daily distance travelled	Yes ($p=0.0004$, $t_{1,27}$=3.75)	Yes ($p=0.0004$, $t_{1,27}$=3.75)	No ($p=0.044$, $t_{2,15}$=-0.08)	Yes ($p=0.017$, $t_{2,14}$=2.33)
Small day range to annual home range ratio	Yes ($p=0.0009$, $t_{1,27}$=-3.34)	Yes ($p=0.0002$, $t_{1,17}$=-4.30)	Yes ($p=0.016$, $t_{2,14}$=-2.38)	Yes ($p=0.01$, $t_{2,14}$=2.58)
Not being predated	Yes ($p=0.012$, $t_{1,38}$=-2.44)	Yes ($p=0.0026$, $t_{1,11}$=-3.46)	Yes ($p=0.0056$, $t_{2,8}$=-3.27)	Yes ($p=0.023$, $t_{2,8}$=2.35)
Low population densities	Yes ($p=0.005$, $t_{1,22}$=-2.81)	Yes ($p=0.085$, $t_{1,12}$=-1.43)	Yes ($p=0.051$, $t_{2,10}$=-1.80)	No ($p=0.122$, $t_{2,10}$=1.23)
Being non-territorial	Yes ($p=0.072$, $t_{1,13}$=-1.55)	Yes ($p=0.0008$, $t_{1,6}$=-5.44)	Yes ($p=0.001$, $t_{2,5}$=-5.81)	No ($p=0.19$, $t_{2,5}$=-0.93)
Group metabolic need	No ($p=0.114$, $t_{1,20}$=1.24)			
Relatively big hippocampi	No ($p=0.305$, $t_{1,5}$=-0.54)			
# dens used/ year	Insufficient data			
Unproductive habitats	To be determined			
Roaming widely to find mates	To be determined			

These factors do not predict AHR our subset of species; therefore they cannot explain why AHR predicts RT

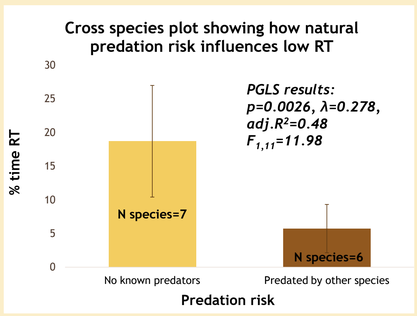
More research to come!

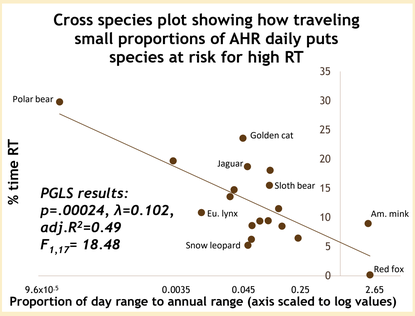
What these results mean:

These factors do predict RT on their own, BUT when combined with AHR in models, AHR proves to drive the effect. Thus these factors cannot explain the relationship between AHR and RT.

Both AHR and these factors predict RT independently. Thus wide ranging species that also possess these traits are most prone to RT.

When combined with AHR in models, the AHR effect vanishes while these factors do predict RT. These factors may therefore explain why AHR predicts RT.





Two species exemplifying this result: The naturally predator-free fossa (*Cryptoprocta ferox*, L)[4] is prone to high levels of RT; while the predated Asiatic black bear (*Ursus thibetanus*, R)[4] is not.

Two species exemplifying this result: The polar bear (*Ursus maritimus*, AHR: 93042.79km^2, L) covers just 0.0092% of its annual range daily in the wild, and shows high levels of RT; while red foxes (*Vulpes vulpes*, AHR: 2.41km^2) traverse their whole annual range two-three times every day, and correspondingly, in captivity show very little RT.

Conclusions: *RT-prone wide rangers may be naturally fearless, autonomous and nomadic*

Analyses are ongoing, but so far, results suggest that high RT Carnivora species are:

- Naturally non-territorial with low population densities;
- Top predators (unlike preyed-on species, familiar terrain with known hiding places is not a priority for them: e.g 3)
- Cover very small fractions of their annual range daily, relocating completely multiple times every year. Perhaps they are therefore novelty-seekers who prefer high levels of control: features that could improve their lives in zoos.

... tend to pace

Background to both studies *b) Our general approach*

- We built on the past work, increasing the route-tracing (RT) database [1,2] to now include c. 2,300 animals across 56 species, 27 with RT data from 5 or more subjects (our focus); expanding the captive infant mortality (IM) database [1,2] to now cover c. 24,500 births across the 56 species; and updating the wild behaviour (WB) database [1,2] plus finding new sources for data on wild carnivore behavioural biology [3,4,6,7].
- For PCMs we used Phylogenetic Generalized Least Squares (PGLS) regressions in R ('Caper') [8] and a recent phylogeny [5].

II. Does foraging niche predict poor welfare in Carnivora?

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Background to the foraging niche study

- Captive Carnivora cannot hunt & kill live vertebrate prey. Does this compromise welfare in naturally hunting-reliant species?
- Evidence in support includes that Carnivora are more prone to RT than other mammals [9]; that long chase distances may be a risk factor (see poster on left); and that RT often peaks pre-feeding.
- But evidence *against* includes that some non-hunters show RT (e.g. giraffes [10] & primates [11]), and that RT peaks at other times too (e.g. when shut indoors during poor weather [12]).
- We therefore used PCMs to resolve this by asking, do aspects of natural foraging niche predict welfare problems across the Carnivora?

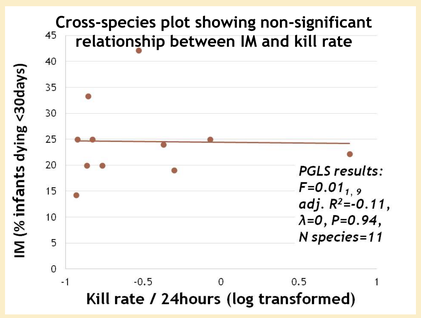
Methods for the foraging niche study

- Our measures of captive welfare were again RT and captive IM (see 2 for details).
- Reliance on hunting was assessed via: kill rate & hunt rate /24hrs (from the updated WB database) and dietary classification [4].
- Hunting style was assessed via: chase distance (m) (from WB database) and hunting strategy [6,7].
- Prey selection effects were assessed via: prey mass:predator's own body mass [13].
- To establish if foraging niche explains the variance in RT not explained by annual home range size (see poster to left), home range data were taken from the WB database.

Results: *Are RT and/or captive IM predicted by …*

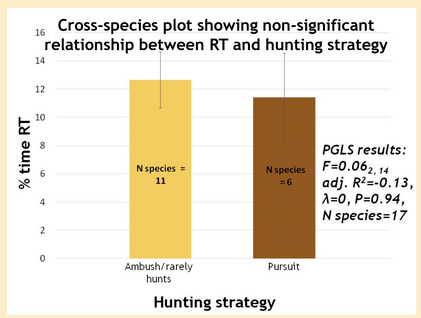
… reliance on hunting in the wild?

NO: *P > 0.39 in all the six models investigating whether hunting intensity predicted RT or IM in captivity. E.g…*



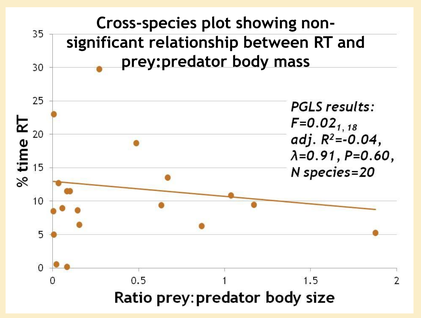
…hunting style?

NO: *P > 0.33 in four models investigating whether captive pursuit predators are most prone to RT or IM. E.g…*



… or hunting large prey?

NO: *P > 0.60 in both models. E.g…*



- **But does statistically controlling for natural range size** *(a major influence: see poster to left)* **reveal effects of foraging niche?**

  Still NO: *P > 0.32 in all models.*

- **And could including foraging niche improve how well ranging predicts RT?**

  NO again: *Adding foraging niche did not improve the fit of any range size models.*

Conclusions: *Natural foraging niche does not predict welfare in captive Carnivora*

Two species exemplifying these findings:
When performing RT, mainly herbivorous (4) giant pandas (L) do so for on average 5.25% of the day. The equivalent value for snow leopards (R), obligate hunters (4), is near identical (5.23%).

- Foraging niche does not predict RT or IM in captive Carnivora. The previous chase distance effect [2] thus seems to have been a Type I error.
- Thus RT is not redirected hunting, and based on the measures used here, hunters do also not seem to have behavioural needs to hunt. This may be because hunting is naturally risky [14], making 'risk-free' food a good option for captive hunters.
- That RT often peaks pre-feeding may simply reflect food anticipation [e.g. 15], with RT perhaps inadvertently being reinforced because the animal is fed.

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